Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters

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Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters

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Abstract

Urban growth is a major factor of global environmental change and has important impacts on biodiversity, such as changes in species composition and biotic homogenization. Most previous studies have focused on effects of urban area as a general measure of urbanization, and on few or single taxa. Here, we analyzed the impacts of the different components of urban sprawl (i.e., scattered and widespread urban growth) on species richness of a variety of taxonomic groups covering mosses, vascular plants, gastropods, butterflies, and birds at the habitat and landscape scales. Besides urban area, we considered the average age, imperviousness, and dispersion degree of urban area, along with human population density, to disentangle the effects of the different components of urban sprawl on biodiversity. The study was carried out in the Swiss Plateau that has undergone substantial urban sprawl in recent decades.

Vascular plants and birds showed the strongest responses to urban sprawl, especially at the landscape scale, with non-native and ruderal plants proliferating and common generalist birds increasing at the expense of specialist birds as urban sprawl grew. Overall, urban area had the greatest contribution on such impacts, but additional effects of urban dispersion (i.e., increase of non-native plants) and human population density (i.e., increases of ruderal plants and common generalist birds) were found. Our findings support the hypothesis that negative impacts of urban sprawl on biodiversity can be reduced by compacting urban growth while still avoiding the formation of very densely populated areas.

Key words:

Built-up area; biotic homogenization; imperviousness; human population density; time-lagged effects; urban dispersion.

Introduction

Land-use change is a central component of global change and a major threat to biodiversity (Sala et al. 2000). Urban growth is in turn an important driver of such land-use changes (Grimm et al. 2008; Elmqvist et al. 2013). The growth of urban areas worldwide was especially pronounced during the second half of the 20th century, but rapid urban expansion still continues and is expected to persist in the next decades as the world's population grows and more people live in cities (Grimm et al. 2008; Mcdonald et al. 2008; Elmqvist et al. 2013).

Species richness has frequently been found to peak at moderate levels of urban development (Rebele 1994; Niemelä 1999; Blair 1999; Crooks et al. 2004). However, not all organisms are equally affected, and the impact of urban growth may noticeably vary depending on species characteristics, such as dispersal ability, habitat specialization, or use of resources (Wood and Pullin 2002; Devictor et al. 2007). The peak in species richness at moderate urbanization levels usually results from an increase in common species adaptable to urban environments, such as early successional plants (Deutschewitz et al. 2003) or generalist animals that take advantage of high habitat heterogeneity and resource availability, as well as low competition or predation rates in urban areas (Savard et al. 2000; Crooks et al. 2004; McKinney 2008). At the same time, some species from the original communities that are sensitive to urban conditions may still survive in the remaining natural or semi-natural habitats, adding to the overall species richness (McKinney 2002, 2006, 2008).

Advanced stages of urbanization, however, usually cause a loss of native specialist in favor of a few urban exploiters, such as ruderal and non-native plants, which tolerate high levels of disturbance (Deutschewitz et al. 2003; Kühn and Klotz 2006; Nobis et al. 2009), or synanthropic animals that depend on human-subsidized resources (Crooks et al. 2004; Devictor et al. 2007). As a result, at high levels of urbanization species richness generally

68 decreases and urban biotas tend to become more and more similar – also called biotic
69 homogenization – dominated by a few common native species and some ubiquitous non-
70 native species (McKinney 2002, 2006; Clergeau et al. 2006; Lososová et al. 2012a, b; Le Viol
71 et al. 2012; Aronson et al. 2014; La Sorte et al. 2014).

72 The spatial scale at which effects of urbanization on biodiversity are analyzed has also been
73 found to be relevant, with impacts like biotic homogenization being more evident at larger
74 spatial scales, both in terms of the extent of the study area and in terms of grain size
75 (Deutschewitz et al. 2003; Kühn and Klotz 2006; La Sorte et al. 2014). However, studies have
76 traditionally focused on particular urban areas, and although some of them have compared
77 urban impacts in different cities across regions, countries, or even continents (see e.g. Pyšek
78 1993; Pyšek 1998; Aronson et al. 2014; La Sorte et al. 2014), large-scale analyses along broad
79 urbanization gradients are still scarce (Devictor et al. 2007; Lososová et al.2012a, b; Le Viol
80 et al. 2012).

81 Most previous studies analyzing urban impacts on biodiversity focused on responses of
82 organisms along urbanization gradients that typically consider increasing proportion of urban
83 area or other urban parameters, such as the degree of imperviousness (i.e., soil sealing) or
84 human population density (see McDonnell and Hahs 2008 for a review). However, most
85 studies lacked reliable measures of other components of the so-called urban sprawl (i.e.,
86 scattered and widespread urban growth; Jaeger et al. 2010). Specifically, the degree of urban
87 sprawl can be estimated with a combined measure of total urban area, intensity of urban land
88 use (e.g., population density), and degree of urban dispersion (Jaeger and Schwick 2014).
89 Besides built-up area (hereinafter referred to as 'urban area') and other characteristics of
90 urban environments, the spatial configuration of urban area, as well as natural or semi-natural
91 areas at the landscape level, may also affect biodiversity (Marzluff and Ewing 2001; Croci et
92 al. 2008; Sattler et al. 2010; Fontana et al. 2011; Latta et al. 2013). Furthermore, time lags

93 may occur before impacts of urban sprawl on biodiversity are apparent (Ramalho and Hobbs
94 2012). However, such delayed effects of urban development have rarely been explored (but
95 see Soga and Koike 2013).

96 Here, we present a comprehensive analysis of the effects of different components of urban
97 sprawl on species richness of various species groups in the Swiss Plateau, which represents
98 the largest biogeographic region of Switzerland (ca. 11,200 km^2) and is affected by severe
99 past and current urban sprawl (Schwick et al. 2012). Overall, we aimed to contribute to a
100 better understanding of the impacts driven by the distinct urban sprawl components on species
101 richness and to generate guidelines for biodiversity monitoring and conservation under future
102 urban development. We addressed the following specific questions: (1) Which types of
103 organisms benefit and which suffer most under urban sprawl? (2) Which attributes or
104 components of urban sprawl have the strongest impacts on species richness? And lastly, (3) at
105 which spatial scales are effects of urban sprawl on biodiversity more evident?

106 We considered five taxonomic groups (i.e., birds, butterflies, terrestrial gastropods, vascular
107 plants, and mosses) that were covered in Swiss biodiversity monitoring programs at varying
108 spatial scales from 10 m^2 (habitat level) to 1 km^2 (landscape level). We evaluated effects of
109 urban sprawl on the species richness of each taxonomic group and of distinct ecological
110 groups defined according to species characteristics that were expected to be sensitive to urban
111 development (e.g., habitat and resource specialization, commonness, dispersal ability). We
112 investigated urban effects along with other environmental variables (climate, topography, and
113 land use) that are known to affect biodiversity. In addition, we used a wide set of urban
114 predictors to disentangle relationships between different components of urban sprawl and
115 species richness. Besides urban area, which was expected to strongly affect species richness,
116 we analyzed the impact of additional urban attributes of likely influence, such as the degree of
117 imperviousness, human population density, urban dispersion, and average age of urban area.

Methods

1) Study area, species richness, and ecological groups

Our study focused on the Swiss Plateau (Fig. 1), the central part of Switzerland between the Alps and the Jura Mountains delimited according to the definition of Swiss biogeographic regions (Gonseth et al. 2001). This region has a mean altitude of 540 m a.s.l. (range: 300–940 m a.s.l.), a mean annual temperature of 8.5 °C (6.5–9.5°C), and a mean annual precipitation of 1140 mm (730–2000 mm). In the Swiss Plateau, agricultural land use predominates (around 50% area), followed by forests (24%) and urban areas (15%). Total urban area has tripled since the beginning of the 20th century, especially between 1960 and 1980 when an increase of around 50% occurred, and is still expected to grow in the future, though at lower rates (Schwick et al. 2012). We analyzed data on species richness of five taxonomic groups (mosses, vascular plants, terrestrial gastropods, butterflies, and birds) regularly collected using a systematic sampling design in the biodiversity monitoring programs of Switzerland (BDM – Biodiversity Monitoring in Switzerland Coordination Office 2009) and of the Canton of Aargau (LANAG; Kanton Aargau 1996). From the BDM program, we used species lists of all available plots in the Swiss Plateau, that is, 109 plots at the landscape level (each 1 km^2 in area; including vascular plants, butterflies, and birds; BDM Z7 indicator) and 473 circular plots at the habitat level (each 10 m^2 in area; including mosses, vascular plants, and gastropods; BDM Z9 indicator; Table 1, Fig. 1). From the LANAG program, we analyzed 436 plots at the habitat level located within the Swiss Plateau (10 m^2 plots for vascular plants and gastropods, 100 m radius-plots for birds, and 250 m transects for butterflies). From both programs, we used data of surveys performed between 2007 and 2011 (see Table A.1 for further details about sampling designs of the different biodiversity monitoring programs).

142 For each taxonomic group and monitoring program, we calculated overall species richness per
143 plot as well as species richness of a variety of ecological groups classified according to
144 species-specific characteristics that we expected to influence species' responses to urban
145 sprawl. Species characteristics were morphological, physiological, or phenological features
146 (functional traits sensu Violle et al. 2007), such as dispersal ability, growth form, and resource
147 use (e.g., diet, habitat use and specialization). Species were additionally classified according
148 to their commonness or rarity (calculated as frequency of occurrence in the dataset), and in
149 the case of vascular plants as native and non-native species. We further classified non-native
150 vascular plant species according to time of introduction (archeophytes and neophytes, i.e.,
151 species introduced in Switzerland by humans before or after 1500 A.D.). Resource range and
152 habitat requirements were used to classify species as specialists or generalists (for a detailed
153 description of species characteristics and classification see Table A.2). To explicitly test for a
154 qualitative shift in species composition along the urbanization gradient, we calculated ratios
155 of generalist to specialist species, very common to rare species, and native to non-native plant
156 species. Threatened species according to Swiss Red Lists were also considered.

157

158 2) Urban sprawl data

159 To describe urban sprawl, we calculated a set of explanatory variables at the different plot
160 scales of the distinct biodiversity monitoring programs (see Table 1 for details). As urban
161 variables, we used urban area (defined as built-up area, i.e., houses, industries, roads, and
162 other infrastructures, but also gardens, parks, and other recreational areas), degree of
163 imperviousness (i.e., soil-sealing), average age of urban area (considered over a period of 125
164 years, i.e. 1885–2010), human population density (number of inhabitants per area), and the
165 spatial dispersion of urban areas. This last variable was quantified using the mean proximity
166 index of urban areas (MPI, with low MPI values meaning high urban dispersion) for larger

plot sizes, or the nearest distance to urban areas in the case of the small plots at the habitat level. Overall, we investigated urban sprawl impacts along a broad urbanization gradient, which covers a range from 0% up to 66% of urban area at the landscape scale (see Table 2 for a detailed description of urban sprawl variables).

We also used other environmental predictors known to affect biodiversity, like climatic, topographic, and additional land use variables (see e.g. Blair 1999; Wood and Pullin 2002; Nobis et al. 2009; Lososová et al. 2012a), which were calculated at the same spatial scale as species richness data to control for possible confounding effects (see Tables 1 and 2 for details).

3) Data analyses

We followed a hierarchical approach to analyze the relationships between urban sprawl and species richness. In a first step, we compared the overall importance of all urban versus all non-urban predictors to explain the variability in species richness for the different taxonomic and ecological groups. Second, for those groups for which urban predictors explained a substantial amount of variability, independently from non-urban predictors, we looked at the effects of individual urban predictors.

For the first step, we performed generalized linear models (GLMs) with species richness of the different taxonomic and ecological groups as response and a Poisson error distribution for count data. For the ratios of generalist to specialist species, very common to rare species, and non-native to native plant species, we applied GLMs with a normal distribution of errors. We used two sets of predictors: (1) all urban variables and (2) all environmental variables other than urban ones (Tables 1 and 2). Pearson's product-moment correlations between single predictors were all below 0.8. To control for possible bias caused by collinearity, we compared results of models both excluding and including human population density, the only

predictor that showed noticeable correlations with other urban predictors ($0.8 \geq r \geq 0.7$; Dormann et al. 2013). Linear and quadratic terms of urban predictors were included in models to account for possible non-linear effects. For every response variable, we then calculated the percentage of null deviance explained by full models (i.e., including the whole set of urban and non-urban predictors; D^2_{full}), the percentage of null deviance (D^2) explained by the two sets of environmental predictors independently ($D^2_{I.Urban}$ and $D^2_{I.Non\text{-}urban}$), as well as their joint contribution to deviance explanation (D^2_J).

In a second step, we examined the individual effects of urban predictors on species richness for those taxonomic and ecological groups that were substantially affected by urban predictors, independent from non-urban predictors ($D^2_{I.Urban} \geq 15\%$). We selected this threshold because it coincided with significant effects ($p \leq 0.05$) of single urban predictors included in full models. We used multi-model inference based on model averaging in order to calculate more robust estimates of the coefficients of urban predictors (Burnham and Anderson 2002). For each response variable, we performed GLMs with all possible combinations of predictors (including both urban and other environmental variables) and ranked them according to the second-order Akaike's information criterion (AICc), or its quasi-likelihood counterpart (QAICc) in cases where over-dispersion occurred. We then selected the most plausible models according to these criteria (delta AICc or QAICc ≤ 4) and calculated averaged parameter estimates using Akaike's weights. To assess the relative contribution of each urban predictor to the overall effects of urban sprawl on species richness, we calculated the relative variable importance (RVI), that is, the sum of Akaike weights that measures the overall likelihood of the selected models in which the parameter of interest appears. RVI values range from 0 (for predictors excluded in all selected models) to 1 (for predictors included in all selected models; Burnham and Anderson 2002). Finally, we used partial residual plots of best-fit models (AIC-based) to graphically illustrate and explore the

direction of significant relationships between distinct urban predictors and species richness. Partial residuals plots of models represent relationships between response variables and an explanatory variable of interest once the effects of all the other predictors have been accounted for.

All statistical analyses were done in R 3.0.2 (R Core Team 2014), using the package MuMIn (Bartón 2013) for model averaging. Urban and non-urban predictors were calculated using the R package raster (Hijmans 2015), as well as ArcGIS and its extension Patch Analyst (ESRI 2011).

Results

Urban predictors explained together and independently of other environmental predictors a substantial proportion of the variability ($D^2_{I.Urban} \geq 15\%$) in species richness of distinct ecological groups of vascular plants and birds. For these groups urban predictors were slightly more relevant than the other environmental variables (23% $D^2_{I.Urban}$ and 20% $D^2_{I.Non\text{-}urban}$ on average; see Table 3 for details). These responses were found almost exclusively at the landscape level (BDM Z7; with 16 responding groups out of 80), with only a few groups of bird species being affected also at the habitat level (LANAG; 3 responding groups out of 82). All these species groups showed significant responses to specific urban predictors (Table 3; for additional details see Tables A.3 and A.4).

Urban area had on average the highest relative variable importance (RVI), followed by human population density, degree of urban dispersion (i.e., mean proximity index of urban areas [MPI] or nearest distance to urban areas), degree of imperviousness, and average age of urban areas (Table 3, Fig. 2). Models excluding human population density as a predictor to control

239 for slight collinearity with other predictors showed consistent results for the remaining urban
240 variables, and therefore we only present the models including the complete set of predictors.

241 For vascular plants, partial regression plots showed along the gradient of increasing urban
242 area a considerable increase in species richness of non-natives, in particular neophytes (Table
243 3, Fig. 3a), specific growth forms (phanerophytes and chamaephytes), and human-dispersed
244 (anthropochorous) plants. In addition, species richness of plants inhabiting eutrophic habitats
245 (Fig. 3b), non-native, habitat specialist, and annual (therophytes) plants increased together
246 with human population density. The degree of urban dispersion had additional positive effects
247 on the ratio between non-native and native plant species and on the species richness of
248 neophytes, phanerophytes, and chamaephytes (i.e., negative effects of MPI; Table 3 and Fig.
249 3c). Last, the degree of imperviousness of urban areas mostly increased species richness of
250 highly dispersive and wind-dispersed (anemochorous) plants (Table 3 and Fig. 3d).

251 Among birds, species groups showing responses relevant to urban sprawl variables were
252 urban, zoophagous, ground breeding, and breeding generalist birds as well as the ratio of
253 breeding generalist to specialist birds. All these groups showed positive responses to urban
254 area and human population density, except ground breeding birds whose species richness
255 significantly decreased with the amount of urban area (see Fig. 4 for examples of the most
256 relevant effects of these variables on birds). When considered at the habitat level, species
257 richness of zoophagous and urban birds and the ratio of breeding generalist to specialist birds
258 significantly decreased as the nearest distance to urban areas increased, whereas the ratio of
259 breeding generalists to specialists increased with the average age of urban areas (Table 3).

260 Species richness of all other ecological and taxonomic groups (i.e., mosses, gastropods and
261 butterflies), including endangered species of the different taxa, showed only weak ($D^2_{I.Urban}$ <
262 15 %) or non-significant responses to urban sprawl variables, and were more strongly affected

263 by non-urban variables (7% $D^2_{I.Urban}$ and 15% $D^2_{I.Non\text{-}urban}$ on average; see Tables A.3 and A.4
264 for details).

265

266 **Discussion**

267 Overall, our study showed important impacts of urban sprawl on species richness of distinct
268 taxonomic and ecological groups. As we hypothesized, these impacts considerably varied
269 depending on the species groups, urban sprawl components and spatial scales considered.

270 1) Taxonomic and ecological groups

271 Time of introduction, dispersal mode, growth form and habitat specialization were the species
272 characteristics that mainly affected the responses of plant species richness to urban sprawl.
273 Non-native species, especially neophytes, benefitted most from urban sprawl, which confirms
274 results of previous studies for our study area (Kühn and Klotz 2006; Nobis et al. 2009;
275 Lososová et al. 2012a).

276 Species richness of plants inhabiting eutrophic places, as well as annual, highly dispersive,
277 wind- and human dispersed plants, also benefitted from urban sprawl (see e.g. Knapp et al.
278 2009). These results are in line with previous findings revealing that native common
279 generalists still predominate in most urban areas (Lososová et al. 2012a, b; Schmidt et al.
280 2013; Aronson et al. 2014).

281 Habitat specialist plants also benefitted from intermediate levels of urbanization covered in
282 our study, probably because of the wide variety of habitats and more extreme environmental
283 conditions in urban areas (Rebele 1994; Niemelä 1999). According to our definition (Table
284 A.2), this group of plants consists of species with narrow ranges of habitat preferences, that is,
285 preferring habitat extremes with respect to temperature, continentality, light, or moisture, pH,
286 nutrients, humus, or aeration of soils. Valued species like native specialist or endangered

287 species are still known to inhabit less-disturbed urban sites (e.g. Kühn and Klotz 2006; Sattler
288 et al. 2010; Fontana et al. 2011; Lososová et al. 2012a; Schmidt et al. 2013). However, we did
289 not find significant responses of these valued species to urban sprawl, likely because they are
290 affected by factors related to local habitat characteristics that were not included in our set of
291 predictors. Likewise, specialist species from rare natural habitats are hardly covered in the
292 distinct biodiversity monitoring programs used in this study, given the broad extension they
293 cover and their regular sampling designs. In addition, whereas colonization by highly
294 dispersive species may more directly track environmental change caused by urban sprawl,
295 species that are negatively affected by urban sprawl may show less clear or direct responses
296 due to the delay in the manifestation of such effects in species richness (i.e., extinction debt;
297 Ramalho and Hobbs 2012; Soga and Koike 2013). Therefore, the positive response of habitat
298 specialists in our study was most probably driven by species occurring in disturbed eutrophic
299 or dry habitats, such as early successional plants, rather than specialist species from rare
300 natural habitats (Knapp et al. 2009). Most habitat specialist plants in our study actually were
301 common species inhabiting eutrophic places (around 70% of species occurrences), and both
302 groups of plants in fact showed similar responses to urban sprawl, being affected most by
303 population density (i.e., intensity of urban land use).

304 Habitat specialization, together with foraging and breeding traits, also had a large influence
305 on birds' responses to urban sprawl. As expected, birds pre-defined as urban benefitted most,
306 confirming the classification developed by the Swiss Ornithological Institute
307 (http://www.vogelwarte.ch/). More interestingly, our results indicate a shift towards breeding
308 generalists, while species richness of ground breeding birds decreased as urban sprawl grew.
309 Breeding specialists, especially ground-nesting birds, tend to be highly sensitive to urban
310 development (McKinney 2002, 2006; Clergeau et al. 2006), whereas birds able to nest in

311 buildings and on other artificial substrates such as cavity and cliff nesters (e.g., swifts, doves,
312 or falcons) benefit from urban areas (Blair 1996; Savard et al. 2000; Chace and Walsh 2006).

313 Species richness of zoophagous birds was also positively affected by urban sprawl, probably
314 driven by ground foragers and aerial insectivores that benefit from the high food availability
315 and the variety of open spaces at the still moderate levels of urbanization gathered in our
316 study (Beissinger 1982; Clergeau et al. 1998; McKinney 2002, 2006; Chace and Walsh 2006).

317 According to additional data from the Swiss Ornithological Institute, the groups of birds that
318 benefitted from urban sprawl hold larger population sizes in Switzerland than those that were
319 negatively affected. Breeding generalist species have on average ca. 122,000 (± 32,000 [SE])
320 breeding pairs, whereas breeding specialists and especially ground breeding specialists in our
321 study have on average only ca. 34,000 (± 7,000) breeding pairs. Birds pre-defined as urban
322 (ca. 90,000 ± 43,000 breeding pairs) or zoophagous (ca. 64,000 ± 12,000 pairs) also exceed
323 the mean population size of the overall set of bird species in our study (ca. 62,000 ± 12,000
324 pairs). Consequently, urban sprawl clearly favored more common generalist birds at the
325 expense of less-abundant specialist species and thus tended to homogenize bird communities
326 (see e.g. Savard et al. 2000; Devictor et al. 2007).

327 Surprisingly, all species groups of mosses, gastropods, and butterflies showed only marginal
328 responses to urban sprawl in our analyses. Lack of response of these groups is probably due to
329 either spatial or temporal constraints in our study that are discussed in depth in the last section
330 of the discussion, and therefore cannot directly be interpreted as a signal of insensitivity to
331 urbanization of these species groups.

332 2) Components of urban sprawl

As expected, urban area had the largest effects, but the other components of urban sprawl also had a great influence. Besides urban area, relevant changes in species richness were also driven by human population density and the degree of urban dispersion.

Human population density in urban areas can be related to the intensity of urban land use and was positively related to groups of birds that are more tolerant of human disturbances. These groups include common generalists with respect to both breeding and foraging requirements, in contrast to more sensitive and specialist species (Blair 1996; Clergeau et al. 1998; Savard et al. 2000; McKinney 2002, 2006). For plants, increased human population density mostly favored species associated with eutrophic habitats. Likewise, degree of imperviousness, which is related to the extent of modification of the previous habitats, favored highly dispersive and wind-dispersed plant species. These species thus tend to occur in intensively used (i.e., human-populated) or altered (i.e., impervious) urban sites and take advantage of modified urban habitats that are maintained at early successional stages by recurrent urban disturbances (Deutschewitz et al. 2003; Kühn and Klotz 2006; Nobis et al. 2009; Lososová et al. 2012a, b).

The spatial configuration of urban areas also had relevant effects on species richness. Increased urban dispersion (measured as mean proximity index [MPI] of urban area) mostly favored the proliferation of non-native plant species, in particular neophytes. Neophytes tend to proliferate in highly dispersed urban areas probably because these regions offer more opportunities for species spread, with the consequent risk of dispersal into rural or semi-natural areas.

With respect to the temporal component of urban sprawl, increased age of urban areas augmented the ratio of breeding generalist to specialist birds at the habitat level. Despite possible effects of building typology and structure related to the age of urban areas, this result might indicate a time lag in the shift from breeding specialists to generalists related to urban

sprawl. Longer (i.e., more delayed) time-lagged effects of urbanization are usually expected for organisms with lower turnover rates, such as birds or perennial plants, compared to short-lived organisms like annual plants (Ramalho and Hobbs 2012; Soga and Koike 2013). Our results partially support this postulate since birds behaved as expected, but we only found marginally significant age-related effects for perennial plants.

3) Spatial scales and constraints

Most effects of urban sprawl on species richness were found at the landscape scale, and only a few groups of birds significantly responded at the habitat scale, demonstrating that larger spatial scales are more appropriate for monitoring impacts of urban sprawl on biodiversity. This is probably due to the small size of plots at the habitat level, especially the 10 m^2 plots, where factors related to local habitat characteristics or land-use intensity and history might be more important than our set of urban predictors, which describe a process occurring at the landscape level. Species groups that showed strong responses at the landscape level, like vascular plants, exhibited no clear responses at the habitat level at all. Hence, the lack of responses of those taxonomic groups that were exclusively surveyed at the habitat level (i.e., mosses and gastropods) may be partly due to the unsuitability of this spatial scale to explore impacts of urban sprawl. This is supported by the fact that birds that were surveyed at a larger habitat scale (3.14 ha plots) in the Canton of Aargau (LANAG) responded similarly to those sampled at the landscape scale (BDM Z7). Together with the typically large home ranges of birds, this finding suggests that responses of birds at the habitat level also reflect what occurs in the surrounding landscape (see e.g. Chace and Walsh 2006).

The absence of a significant impact of urban sprawl for some groups of organisms (mosses, gastropods, butterflies, or endangered species), however, might also be due to strong declines in species richness of these groups between 1950 to 1980 due to large-scale changes and intensification of land uses in our study region (Lachat et al. 2010). Hence, past large-scale

383 declines of these taxonomic groups are likely to be masking potential urbanization signals in
384 the present. Specifically in the case of butterflies, we did not find clear responses to urban
385 variables at the landscape or at the habitat level. These results contradict previous studies that
386 have found this taxon to be highly sensitive to the loss of natural and semi-natural habitats
387 due to the expansion of urban areas and intensive agriculture (e.g. Blair 1999; Wood and
388 Pullin 2002; Stefanescu et al. 2004; Altermatt 2012; Casner et al. 2014). However,
389 contemporary levels of butterfly species richness in our study region are likely so low that no
390 further urbanization impacts are detectable. Mean species richness of butterflies per plot in
391 our dataset (22.4 species in landscape plots) was indeed lower than for those groups that
392 markedly responded to urban sprawl (i.e., plants and birds, with 248.4 and 40.2 species per
393 plot, respectively).

394 Meta-community dynamics of butterflies that move across dispersed patches of suitable
395 habitat in the landscape are probably influencing their responses to urban sprawl as well, so
396 that urban impacts may only be evident at even larger spatial scales than those considered in
397 our study (1 km^2). Most studies showing urban impacts on butterfly diversity actually
398 measured urbanization levels in large areas around the sites where diversity data were
399 gathered (e.g., 5–10 km radius buffers; Stefanescu et al. 2004; Casner et al. 2014).

400 Lastly, due to the fact that our study did not cover a whole urban gradient our survey,
401 reaching only maxima of 66% urban area at the landscape scale (see Table A.5 for details),
402 impacts of urban sprawl on species richness at the end of the urban gradient (i.e., completely
403 urbanized areas) were not explored and may have been unnoticed. Nevertheless, our approach
404 allowed us to investigate the impacts of urban sprawl in the transition from rural to urban
405 landscapes, where most relevant impacts on biodiversity are expected to occur (Miller and
406 Hobbs 2002; Mcdonald et al. 2008). The absence of response of some groups of organism,
407 probably because of either spatial (i.e., unsuitable scale of analysis) or temporal (i.e.,

408 remarkable impacts happened in the past) constraints, also suggests that some impacts of
409 urbanization may have gone undetected. These facts compel us to be cautious in the
410 interpretation of our results, even more so if we consider possible time-lagged effects. A
411 broader spatio-temporal perspective might thus be required to find relevant impacts of urban
412 sprawl for groups that seemed to be unaffected in our analyses.

413

414 **Conclusions**

415 Urban sprawl was a strong predictor of species richness for distinct groups of plants and birds
416 in the Swiss Plateau. It mostly related to the proliferation of non-native, especially neophyte,
417 and ruderal plant species, as well as to the replacement of specialist birds with more common
418 and generalist species, and thus to the homogenization of species assemblages. Moreover, we
419 found that most impacts of urban sprawl were driven by the increase in urban area, but
420 interestingly other components of this process greatly contributed to these impacts as well. In
421 particular, the increases of ruderal plants and common generalist birds were highly related to
422 the intensity of urban land use, whereas the spread of non-native plants was strongly related to
423 urban dispersion. These results pointed out the negative impacts of urban spreading into
424 natural or semi-natural areas on biodiversity. In the context of the current discussion on urban
425 dispersion versus densification, the latter seems preferable (see also Soga et al. 2014). Hence,
426 new urban areas should be developed close to already urbanized areas rather than dispersed
427 into rural landscapes. However, such new developments should also provide enough high-
428 quality open spaces (i.e., parks, gardens and other green areas) that soften urban land use
429 intensity in order to support biodiversity and concurrently foster residents' welfare (e.g.,
430 Miller and Hobbs 2002; Sattler et al. 2010; Fontana et al. 2011). Even though dense urban
431 development may reduce opportunities for people to live close to nature, it facilitates public
432 access (Sushinsky et al. 2013). Finally, if we consider present rates of land consumption by

433 urban development, both worldwide (Grimm et al. 2008; Mcdonald et al. 2008) and
434 particularly in our study region (Schwick et al. 2012), and the likely time lag in the
435 manifestation of some impacts of urban sprawl on biodiversity (Ramalho and Hobbs 2012),
436 the balance inclines towards an urban densification. Upper limits of urban densification have
437 however to be carefully investigated taking together into account biodiversity conservation
438 and human quality of life.

439

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448

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Table 1. Details on species data from the different monitoring programs operating in the study areas at the habitat and landscape scales. The set of urban and other environmental predictors (i.e., climate, topography and land use) tested for each taxonomic group and monitoring program is provided. See also Table 2.

Spatial scale	Biodiversity monitoring program	Study area	Plot size	Taxonomic group	Urban variables	Other environmental variables
Habitat	BDM Z9	Swiss Plateau	10 m^2	Mosses Vascular plants Gastropods	Urban area Age of urban area Imperviousness Human population density Nearest distance to urban areas (urban dispersion)	Mean annual temperature Mean annual precipitation Aspect Slope (surface roughness) Forest area
	LANAG	Swiss Plateau of the Canton of Aargau	10 m^2	Vascular plants Gastropods		
			3.14 ha (100 m-radius buffers)	Birds		
			78.54 ha (250 m-transects around plot centers within 500 m-radius buffers)	Butterflies	Urban area Age of urban area Imperviousness degree Human population density Mean proximity index (MPI) of urban area (urban dispersion)	Mean annual temperature Mean annual precipitation Aspect Standard deviation ofaltitude (surface roughness) Forest area
Landscape	BDM Z7	Swiss Plateau	1 km^2	Vascular plants Butterflies Birds		

Table 2. Definitions and data sources of environmental predictors, including variables describing urban sprawl and other environmental variables for the plots of the distinct biodiversity monitoring programs at the habitat level (BDM Z9 and LANAG) and landscape level (BDM Z7). See also Table 1.

Predictor	Definition	Data source
Urban variables:		
Urban area	Proportion of plot area occupied by houses (including gardens), roads and other infrastructures, industries, parks and recreational areas, used for BDM Z7 plots and for butterflies in LANAG plots. Location in urban area, used for BDM Z9 plots and for LANAG plots (except butterflies)	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung / (2010, 15 m resolution)
Age of urban area	Average age (weighted by area) of urban areas (in years) using 2011 as reference year, calculated from data on urban areas at different time points (1885, 1935, 1960, 1980, 2002 and 2010)	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung / (time series: 1885–2010; 15 m resolution)
Imperviousness of urban area	Degree of soil-sealing of urban area (%)	Pan-European Copernicus Land Monitoring Services http://www.copernicus.eu/ (2009, 20 m resolution)
Human population density in urban area	Number of human inhabitants (residents) per ha of urban area	Swiss Federal Statistical Office http://www.statistics.admin.ch/ (2011, 100 m resolution)
Mean proximity index (MPI) of urban area	Degree of dispersion of urban area (low MPI values = high dispersion), calculated as the ratio between the mean size of urban patches and the nearest neighbor distance to other urban patches (dimensionless). Used for BDM Z7 plots and for butterflies from LANAG plots	Die Geographen schwick + spichtig http://www.wsl.ch/info/fokus/zersiedelung / (2010, 15 m resolution)
Nearest distance to urban areas	Distance from plots to the nearest neighbor urban area (m). Used for BDM Z9 plots and for LANAG plots (except butterflies)	
Non-urban variables:		
Mean annual temperature	Average value of monthly mean temperatures (°C)	Swiss Federal Office of Meteorology and Climatology http://www.meteoswiss.ch (Data averaged for the period 1961–1990, at 25 and100 m resolution for the habitat and landscape scales, respectively)
Annual precipitation	Sum of monthly precipitation (mm)	
Northness (aspect)	Orientation or direction to which slope faces, ranges from 1 (north-	Swiss Federal Office of Topography

	facing slope) to -1 (south-facing slope)	http://www.swisstopo.ch/ (Data at 25and100 m resolution for the habitat and landscape scales, respectively)
Surface roughness	Standard deviation (SD) of altitude (m a.s.l.), used for BDM Z7 plots and for butterflies in LANAG plots. Slope (surface inclination relative to horizontal, 0–90°), used for BDM Z9 plots and for LANAG plots (except butterflies)	
Forest area	% plot area occupied by forest, used for BDM Z7 plots and for butterflies in LANAG plots. Location in forest area, used for BDM Z9 plots and for LANAG plots (except butterflies)	Federal Statistical Office (FSO) Land use statistics (2004/09, 100 m resolution) http://www.bfs.admin.ch/

Table 3. Results of the two steps of analysis. Step 1: Model performance D^2_{full} of the full models, i.e., percentage of null deviance explained by urban and non-urban predictors, and the corresponding values $D^2_{I.Urban}$, i.e., the percentage of null deviance independently explained by urban predictors based on hierarchical partitioning. All species groups with $D^2_{I.Urban} \geq 15\%$ are shown. Step 2: Relative variable importance (RVI) of single urban predictors from multi-model averaging. Values are provided for urban predictors included in best fitted models (delta AICc or QAICc ≤ 4) for each diversity variable. Arrows indicate the direction of effects (positive ↗ and negative ↘) based on partial regression plots of the best fitted model (AIC-based) and coefficients estimates which are significantly different from zero (P<0.05; values in bold).

	Step 1: Deviance partitioning		**Step 2: Multi-model averaging & partial regressions**				
Species group (Monitoring program)	**D^2_{full} (%)**	**$D^2_{I.Urban}$ (%)**	**Urban area**	**Population density**	**Dispersion**	**Imperviousness**	**Average age**
Vascular plants							
Non-native plants (BDM Z7)	64.2	28.4	**0.45 (↗)**	**0.97 (↗)**	0.22	**0.42 (↗)**	0.03
Neophytes (BDM Z7)	61.8	41.9	**1.00 (↗)**	**0.97 (↗)**	**1.00 (↘)**	0.12	0.07
Ratio non-native *vs.* native plants (BDM Z7)	66.4	17.7	**0.67 (↗)**	**0.69 (↗)**	**0.64 (↘)**	0.07	-
Habitat-specialist plants (BDM Z7)	43.8	15.7	-	**0.67 (↗)**	0.03	**0.43 (↗)**	0.02
Phanerophytes (BDM Z7)	42.6	19.3	**0.98 (↗)**	0.07	**1.00 (↘)**	**0.13 (↗)**	0.17
Chamaephytes (BDM Z7)	29.8	24.5	**0.51 (↗)**	0.01	**0.83 (↘)**	0.03	0.07
Therophytes (BDM Z7)	61.9	16.9	**0.24 (↗)**	**0.49 (↗)**	-	**0.41 (↗)**	0.02
Eutrophic-habitat plants (BDM Z7)	52.9	24.1	-	**0.97 (↗)**	0.04	**0.41 (↗)**	**0.05 (↘)**
Anemochorous plants (BDM Z7)	42.0	17.4	-	-	0.07	**1.00 (↗)**	0.10
Anthropochorous plants (BDM Z7)	45.2	29.7	**1.00 (↗)**	-	0.05	0.18	-
Highly dispersive plants (BDM Z7)	42.0	16.1	0.05	**0.11 (↗)**	0.05	**0.95 (↗)**	0.12
Birds							
Zoophagous birds (BDM Z7)	36.2	23.4	-	**1.00 (↗)**	0.03	-	-
(LANAG)	27.3	18.5	**0.96 (↗)**	0.03	**0.96 (↘)**	0.07	0.03
Ground-breeding birds (BDM Z7)	28.6	15.0	**0.92 (↘)**	0.06	0.12	-	0.04
Urban birds (BDM Z7)	39.2	29.5	**0.76 (↗)**	**0.29 (↗)**	0.02	-	0.05
(LANAG)	37.9	31.7	**1.00 (↗)**	0.03	**1.00 (↘)**	0.05	0.04
Breeding-generalist birds (BDM Z7)	25.7	15.4	0.05	**0.54 (↗)**	0.02	0.04	0.05
Ratio breeding-generalist vs. specialist birds (BDM Z7)	31.0	24.2	**1.00 (↗)**	0.02	0.21	0.02	-
(LANAG)	41.7	28.9	0.02	**1.00 (↗)**	**0.75 (↘)**	0.14	**1.00 (↗)**

Figure 1. Delimitation of study area within Switzerland (thin boundary line), i.e. the Swiss Plateau (thick solid boundary line; Gonseth et al. 2001), and the location of plots from the different monitoring programs are shown: BDM Z7 indicator *Species Diversity in Landscapes* (large dots; 109 plots of 1 km^2); BDM Z9 indicator *Species Diversity in Habitats* (small dots; 473 circular plots of 10 m^2); and LANAG program of the canton of Aargau (denser small dots; 436 plots of different sizes at the habitat level in the Swiss Plateau). The location of the main cities within the study area are indicated in grey.

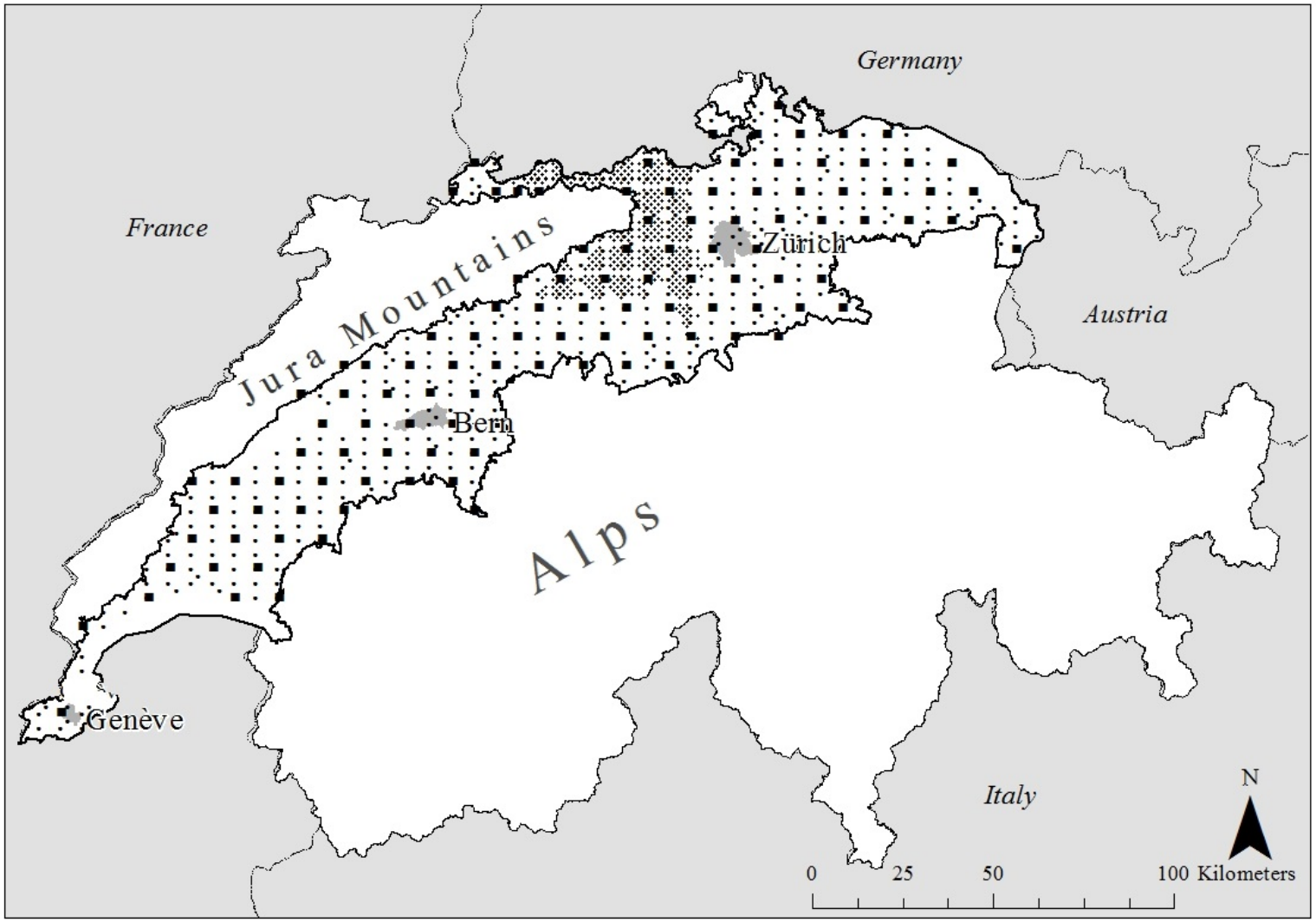
Figure 2. Average (±SE) relative variable importance (RVI) of the different urban predictors (i.e., urban area, population density, dispersion, imperviousness, and average age of urban area) to explain the variation in species richness variables for all species groups that showed relevant responses to urban sprawl ($D^2_{I.Urban} \geq 15\%$) independent from other environmental predictors (see Table 3). Averaged-values are shown for all these groups (grey) and for the subsets of groups for vascular plants (white) and birds (black).

Figure 3. Partial residual plots of significant responses of species richness to single components of urban sprawl at the landscape scale for (a) neophytes and urban area (linear term), (b) plants from eutrophic habitats and human population density of urban area (linear and quadratic terms), (c) neophytes and urban disperson (MPI) (linear term), and (d) highly dispersive plants and imperviousness (linear term). Partial residual plots represent the estimated relationships between response variables and a predictor of interest (solid lines; ±1 SE, dotted lines) once the effects of other predictors have been accounted for. Mean values of species richness per plot (avg.sr) are provided to contextualize the size of effects.

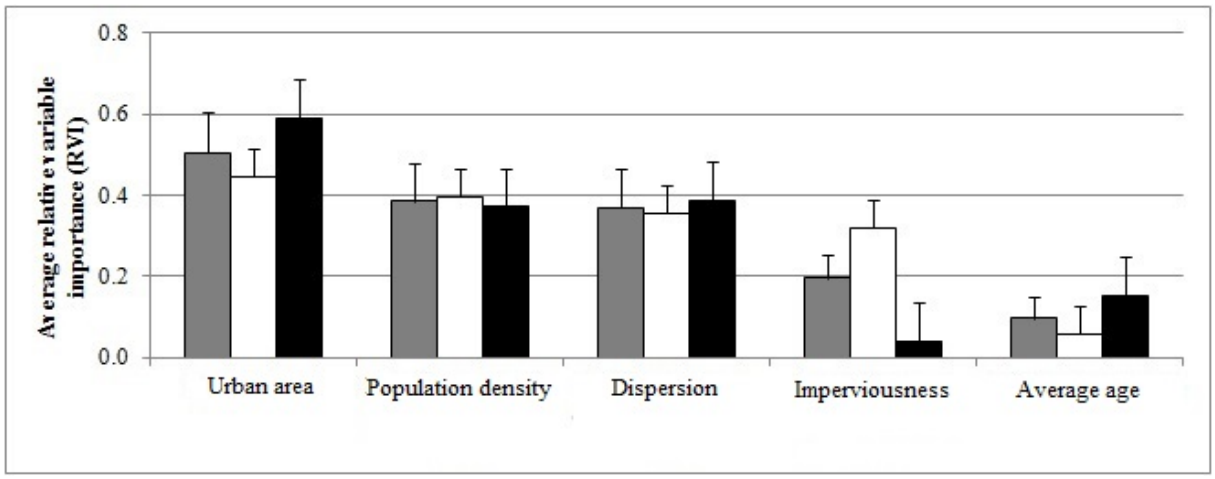
Figure 4. Partial residual plots of significant responses of birds to single components of urban sprawl at the landscape scale for (a) species richness of ground breeding birds to urban area,

and (b) the ratio of breeding generalist to specialist bird species to urban area (linear terms). For further details on partial residual plots see Figure 3.

Concepción et al., Figure 1

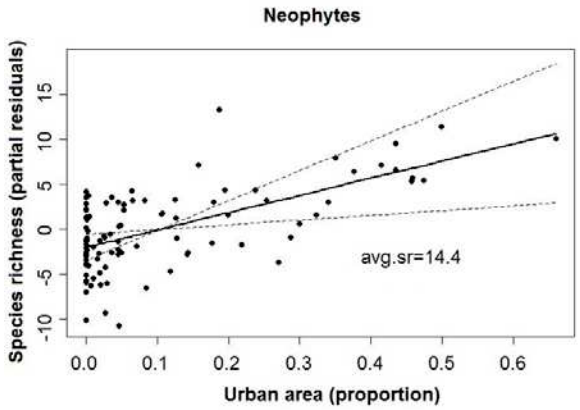


Concepción et al., Figure 2

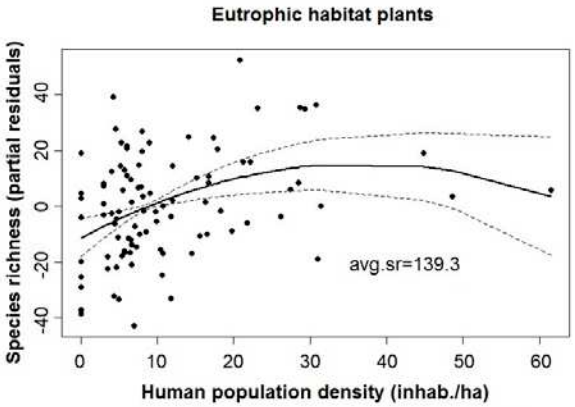


Concepción et al., Figure 3

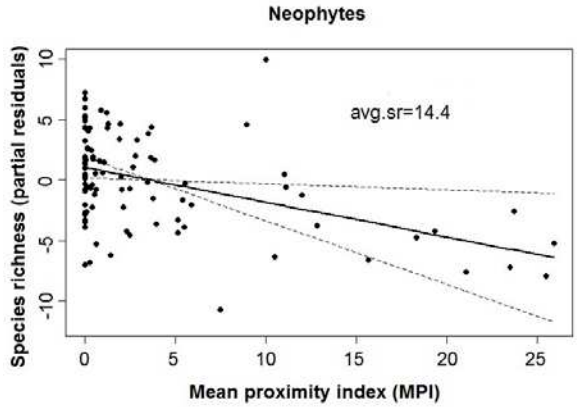
a)



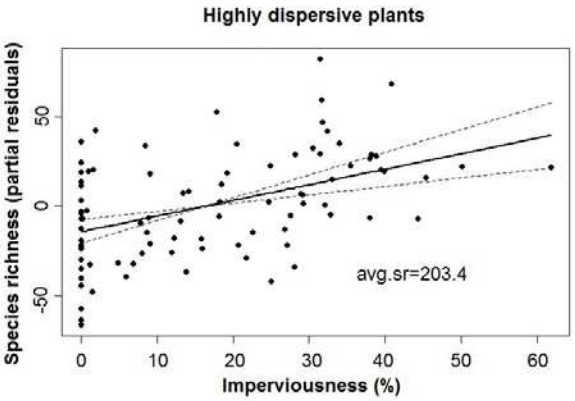
b)



c)



d)



Concepción et al., Figure 4

a) **b)**